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LARGER ECTOPARASITES OF THE IDAHO GROUND SQUIRREL (*SPERMOPHILUS BRUNNEUS*)

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ABSTRACT.—We sampled both subspecies of the Idaho ground squirrel (*Spermophilus brunneus*) to document the larger ectoparasites of this rare endemic. *S. b. brunneus* was host (+ = new host record, * = new Idaho record) to 4 flea species (*Neopsylla inopina*+, *Oropsylla idahoensis*+, *O. tuberculata,* and *Thrassis pandorae*+), 1 tick (*Ixodes sculptus*+), and an eyeworm (Nematoda: *Rhabditis orbitalis**+, also 1st records from Sciuridae); *S. b. endemicus* was host to a louse species (*Neohaematopinus laeviusculus*+), 5 flea taxa (*Rhadinopsylla* sp.+, *O. t. tuberculata, Thrassis f. francisi*+, *T. f. barnesi*+, and *T. f. rockwoodi*), and a mite (*Androlaelaps fahrenholzi*+). *Spermophilus brunneus* had fewer known ectoparasite species than other congeners. Although all of their parasites had many other hosts, *S. b. endemicus* and *S. b. brunneus* shared only a single parasite species in common, whereas all but one of their ectoparasites also occurred on the closely related Townsend's ground squirrel (*S. townsendii*). The proportion of parasitized individuals and the parasite loads per individual were significantly lower in *S. b. brunneus*, which lives in small, isolated populations, than in *S. b. endemicus*, which has larger, less fragmented populations, suggesting a relationship between host population structure, parasite loads, and parasite species diversity. All but one of the flea species have been linked to plague transmission.

Key words: ground squirrels, ectoparasites, Spermophilus brunneus, *Idaho.*

The Idaho ground squirrel (*Spermophilus brunneus*) is one of the rarest and, until recently, least known North American mammals (Sherman 1989, Yensen 1991, Yensen and Sherman in press). This endemic species inhabits a 125 × 90-km area in west central Idaho, but it actually occupies only a small fraction of this limited range (Yensen 1991). Despite the species' restricted geographic distribution, there are 2 allopatric subspecies that are morphologically and genetically differentiated and possibly have reached species-level separation (Yensen 1991, Gill and Yensen 1992, Gavin et al. submitted).

Spermophilus b. brunneus occurs in montane meadows surrounded by coniferous forests at elevations of 1035 to 1550 m in Adams and Valley counties (Yensen 1991). As of 1995, only 18 of the 28 known populations remained, and only one of these contained >100 animals. The majority of the sites were within an area of 22 × 9 km and totaled <300 ha of occupied habitat (T. A. Gavin, P. W. Sherman, and E. Yensen unpublished data).

Fire supression began in the area about 100 yr ago. Subsequent succession and expansion of forests has filled in many of the natural meadows in the range of *S. b. brunneus* (Truksa and Yensen 1990), eliminating habitat. The remaining populations are presently isolated from each other by the encroachment of conifers into meadows and by competition with Columbian ground squirrels (Yensen and Sherman in press). Today, there is apparently little or no gene flow among populations. Allozyme analyses of 55 protein loci in 12 populations (Gavin et al. submitted) indicated that the proportion of polymorphic loci was 11.5%–19.2% and heterozygosity values were 0.041–0.080. F_{st} was 0.317, implying that there is genetic differentiation among populations despite their geographic proximity and the apparent recency of their separation. In 1993 the total number of individual *S. b. brunneus* was 1000–1200, but the number fell to 600–800 in 1994 and 1995 (T. A. Gavin, P. W. Sherman, E. Yensen personal observation).

Spermophilus b. endemicus occurs in rolling foothills at elevations of 670 to 975 m in Gem, Payette, and Washington counties (Yensen 1991). It is patchily distributed throughout its range of 75 × 30 km. Although censuses of *S. b. endemicus* populations have not been made, its total population is apparently much larger than that of *S. b. brunneus*. The area occupied, estimates of population densities, and the amount

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of remaining habitat are more than 2 orders of magnitude greater than for *S. b. brunneus* (E. Yensen personal observation).

Parasites of *S. brunneus* have not been previously surveyed. The only prior records (Baird and Saunders 1992) were 2 flea species, *Oropsylla t. tuberculata* and *Thrassis francisi rockwoodi*, collected from specimens now referred to *S. b. endemicus* (Yensen 1991).

We were interested in how ectoparasite diversity and density are affected by reduction in size and isolation of host populations. According to epidemiological models (Anderson and May 1979, May and Anderson 1979), the number of contacts between hosts and infective stages of parasites determines the rate at which adult parasites are acquired. Mean parasite load should equal growth rate of the population divided by mortality from the disease. Thus, as population growth slows, parasite load per individual should drop. At very low host population densities, there may be too few contacts even to maintain ectoparasite populations. Thus, we predicted that *S. b. brunneus* should have fewer ectoparasite species and fewer ectoparasites per individual than congeneric, more widely distributed western ground squirrels (*Spermophilus* spp.). We also predicted that due to its fragmented population structure and smaller population sizes, *S. b. brunneus* should have fewer ectoparasite species than *S. b. endemicus*.

Because of questions about the taxonomic similarity of *S. b. brunneus* and *S. b. endemicus*, we also wished to learn if they had similar ectoparasites, and how similar their ectoparasites were to those of other western ground squirrels. Further, because of the limited geographic range and low number of small populations, both subspecies of *S. brunneus* would be vulnerable to extirpation by an epizootic such as plague. Thus, it was important to learn if their ectoparasites were species involved in plague transmission.

METHODS

From 1980 to 1990, specimens of *S. brunneus* were collected for a taxonomic study (Yensen 1991). To minimize negative impacts on small populations, a mean of 0.5 individuals/site/yr of *S. brunneus* was collected. Squirrels were killed by shooting or by live-trapping and injecting nembutol into the heart. Immediately postmortem, squirrels were placed individually in plastic bags; fleas, ticks, lice, and larger mites were collected with forceps or a camel's hair brush moistened with 70% ethanol as they left the host. Squirrels were not examined under a dissecting microscope, so smaller mites were not collected; eyes were not examined for eyeworms.

From 1987 to 1994, *S. b. brunneus* were live-trapped for demographic and behavioral studies (Sherman 1989, and ongoing). They were hand-held and parasites were picked off with forceps; because the animals were not anesthetized, all of the smaller and some of the larger ectoparasites may not have been seen. Eyes were checked for eyeworms by pulling back the upper lid; specimens were removed from the cornea of the eye with a cotton swab moistened with sterile water. All parasites were placed in 70% ethanol. In addition, 21 *S. b. endemicus* were live-trapped at Sand Hollow, Payette County, Idaho, in 1994 and examined for eyeworms.

Collected specimens of *S. brunneus* were prepared as standard museum study skins and skulls and deposited in the Albertson College Museum of Natural History (ACMNH), Caldwell, Idaho, and the National Museum of Natural History (USNM); they are identified below by museum number. Specimens of ectoparasites were sent to appropriate specialists for identification and deposited in the entomological collections at the University of Idaho, Moscow, and ACMNH. Differences in parasite loads between individuals and subspecies were analyzed with hand-calculated Mann-Whitney *U*-tests and chi-square tests, as appropriate.

RESULTS

We examined 29 freshly collected individuals of *S. b. brunneus* and 53 of *S. b. endemicus* for ectoparasites. These represent 43% of the 192 museum specimens of this species known to us (Yensen 1991, plus 4 additional specimens). Additionally, we opportunistically collected ectoparasitic arthropods from 12 live-trapped individuals of *S. b. brunneus* and eyeworms from another 36; we examined 21 *S. b. endemicus* for eyeworms.

We collected 6 ectoparasite species from *Spermophilus b. brunneus*: 4 fleas, 1 tick, and 1 nematode (Table 1). We collected 7 taxa of ectoparasites from *S. b. endemicus*: 5 fleas, 1 louse, and 1 mite.

Table 1. Parasites of *S. brunneus* that also occur on some other species of western ground squirrels (subgenus *Spermophilus*). Symbols: * = known primary host(s); + = records, possibly accidental on host; – = no records in references below[a].

	Host									
	This study		Literature records[b]							
Parasite	Sbb	Sbe	Sto	Scc	Sbl	Sar	Sel[c]	Sri	Swa	Spy
Lice										
Neohaematopinus laeviusculus	–	+	+	+	–	+	+	+	–	+
Fleas										
Neopsylla inopina	+	–	+	+	+	+	+	+	–	–
Oropsylla idahoensis	+	–	+	*	*	*	*	+	–	*
O. t. tuberculata	+	+	+	+	+	+	–	+	+	–
Rhadinopsylla s. sectilis	–	?	+	–	–	–	–	–	+	–
Thrassis f. barnesi	–	+	+	–	–	+	+	–	–	–
T. f. francisi	–	+	*	–	+	+	–	–	–	–
T. f. rockwoodi	–	+	+	–	*	–	+	–	–	–
T. p. pandorae	+	–	+	+	*	*	*	+	+	–
Ticks										
Ixodes sculptus	+	–	+	+	+	+	+	+	–	–
Mites										
Androlaelaps fahrenholzi	–	+	+	+	–	+	+	+	–	+
Nematoda										
Rhabditis orbitalis	+	–	–	–	–	–	–	–	–	–

[a]From records in Hubbard (1947), Burgess (1955), Stark (1970), Hilton and Mahrt (1971), Whitaker and Wilson (1974), Holekamp (1983), Lewis et al. (1988), Baird and Saunders (1992), Baird (unpublished), and this study.

[b]Host acronyms: Sbb = *Spermophilus b. brunneus*, Sbe = *S. b. endemicus*, Sto = *S. "townsendii"* (sensu latu), Scc = *S. columbianus*, Sbl = *S. beldingi*, Sar = *S. armatus*, Sel = *S. elegans*, Sri = *S. richardsonii*, Swa = *S. washingtoni*, Spy = *S. parryii*.

[c]Confused in the literature with *S. richardsonii*. The records here are those that unambiguously refer to this species, and the total for *S. richardsonii* may include a few parasites of this species.

The proportion of parasitized individuals in the 2 subspecies was strikingly different. We found ectoparasites on 37 of 53 (70%) *S. b. endemicus* but on only 8 of 29 (28%) *S. b. brunneus* collected ($\chi^2 = 13.4$, d.f. = 1, $P < 0.001$).

Parasitized individuals of *S. b. brunneus* had 1–3 species of ectoparasites each ($\bar{X} = 1.75$, $n = 8$), and parasitized individuals of *S. b. endemicus* had 1–4 species of ectoparasites ($\bar{X} = 1.59$, $n = 37$). This difference was not significant ($U_s = 154$, $P > 0.5$). However, there was a significant difference between subspecies in the parasite load of parasitized individuals. Fleas were the only common group of ectoparasites of both ground squirrel taxa. There were 4.1 fleas per parasitized individual in *S. b. brunneus* and 7.8 in *S. b. endemicus* ($U_s = 95.5$, $P < 0.05$).

Annotated List of Ectoparasites

In the ectoparasite species accounts below, letters and numbers in brackets refer to the number of male and female fleas, e.g., [1 m, 2 f], or to conversions of original collecting data to latitude, longitude, and metric units.

Anopleura: Haematopinidae

Neohaematopinus laeviusculus (Grube)

We found this louse on *S. b. endemicus* in the following locations: 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 222), 28 February 1982 (ACMNH 226, 227, 236, 237, 238); 0.1 mi E Payette Co. line, 12.6 mi [20 km] N Emmett, Gem Co., T8N, R2W, Sec. 12 [44°03′N, 116°32′W, 810 m elev.], 28 February 1982 (ACMNH 224); Weiser Cove, Washington Co. [44°13′N, 116°44′W, 715 m elev.], 7 March 1982 (ACMNH 228, 229, 230); lower Mann Creek, 2.5 mi [4 km] N jct. Weiser River Road, Washington Co. [44°16′N, 116°51′W, 720 m elev.], 14 March 1982 (ACMNH 231, 240, 242, 243, 244).

This louse occurs from Eurasia east to Alaska and the Northwest Territories, and south through western United States to Mexico; it is apparently a species complex (K. C. Emerson personal communication). Lice of this complex have been collected from many ground squirrels (Eurasian *Spermophilus major, S. citellus, S. pygmaeus, S. undulatus*, and North American

S. beecheyi, *S. armatus*, *S. beldingi*, *S. columbianus*, *S. parryii*, *S. townsendii*, *S. washingtoni*, and *Ammospermophilus leucurus*), as well as marmots (*Marmota flaviventris*), chipmunks (*Tamias minimus*), pocket mice (*Perognathus parvus*), and deer mice (*Peromyscus maniculatus*; Rayburn et al. 1975, Shaw and Hood 1975, records from National Museum of Natural History). Although *N. laeviusculus* is the most common louse species taken from ground squirrels in Idaho (C. R. Baird personal communication, K. C. Emerson personal communication), *S. b. endemicus* is a new host record.

Siphonaptera: Hystrichopsyllidae

Neopsylla inopina Rothschild

We collected 8 individuals of this flea from *S. b. brunneus* in the following locations: Lick Creek, Adams Co., T19N, R3W, Sec. 14 [44°59′N, 116°40′W, 1290 m elev.], 17 April 1983 (ACMNH 305 [1 m, 2 f], ACMNH 306 [1 f]); 1 mi [1.6 km] NE Bear Guard Station, Adams Co. [45°05′N, 116°37′W, 1480 m], 2 June 1988 (ACMNH 518 [1 f]); and Price Valley [45°01′N, 116°26°W, 1270 m elev.], 3 June 1981 (ACMNH 209 [1 m, 1 f], ACMNH 210 [1 f]).

This flea occurs from British Columbia south to Oregon and Nevada and east to Saskatchewan, North Dakota, and Utah (Lewis et al. 1988). It has been collected from other western ground squirrels of subgenus *Spermophilus* (Table 1) and from badger (*Taxidea taxus*) dens (Lewis et al. 1988, Baird and Saunders 1992); *S. b. brunneus* is a new host record.

Rhadinopsylla sp.

We collected 1 female specimen of this flea genus from *S. b. endemicus*. Unfortunately, it could not be identified to species. The locality was Dry Creek Road, Payette Co., 1.4 mi [2.2 km] E Little Willow Creek, T9N, R2W, Sec. 18 [44°07′N, 116°37′W, 815 m elev.], 26 February 1983 (ACMNH 318 [1 f], reported in Baird and Saunders 1992).

The flea is most likely *R. s. sectilis*, which occurs in many western states on deer mice (*Peromyscus* sp.) and ground squirrels, including *S. townsendii* and *S. washingtoni* (Lewis et al. 1988, Baird and Saunders 1992). *Rhadinopsylla* are uncommon fleas and have population peaks in the colder months (Lewis et al. 1988). This is the 1st record of any *Rhadinopsylla* species from *S. brunneus*.

Siphonaptera: Ceratophyllidae

Oropsylla idahoensis (Baker)

This flea species was collected on *S. b. brunneus* at the following locations: Price Valley [45°01′N, 116°26°W, 1270 m elev.], 3 June 1981 (ACMNH 209 [3 f]); and OX Ranch 1–2 km S, 1–2 km E Bear, Adams Co. [45°00′N, 116°39′W, 1340 m elev.] (live-trapping collections).

Oropsylla idahoensis occurs from Alaska to New Mexico and is one of the most common fleas of ground squirrels in the Rocky Mountains and westward. Hosts include other western ground squirrels of subgenus *Spermophilus* (Table 1), golden-mantled ground squirrels (*S. lateralis*), and marmots (*Marmota* sp.; Lewis et al. 1988, Baird and Saunders 1992); *S. b. brunneus* is a new host record.

Oropsylla tuberculata tuberculata (Baker)

This was the most common flea on both *S. b. brunneus* and *S. b. endemicus*, occurring at nearly all locations from which we collected ectoparasites. We found *O. t. tuberculata* on *S. b. brunneus* at the following localities: Price Valley [45°01′N, 116°26°W, 1270 m elev.], 3 June 1981 (ACMNH 209 [1 m], ACMNH 210 [1 m]); Mill Creek summit, 5 km N Hornet Guard Station, Adams Co., T18N, R3W, Sec. 25, 4500′ elev. [44°53′N, 116°39′W, 1370 m], 2 June 1985 (ACMNH 510 [2 m, 3 f], ACMNH 512 [2 m, 3 f]); Lick Creek, Adams Co., T19N, R3W, Sec. 14 [44°54′N, 116°40′W, 1290 m elev.], 17 April 1983 (ACMNH 305 [4 m, 3 f], ACMNH 306 [1 f]); Round Valley, Valley Co. [44°21′N, 116°00′W, 1460 m elev.], 18 May 1985 (ACMNH 315 [1 f]).

Records from *S. b. endemicus* are as follows: Sucker Cr. 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 221, 222, 223), 28 February 1982 (ACMNH 225, 226, 227), 3 May 1987 (ACMNH 544 [1 m]); 0.1 mi E Payette Co. line, 12.6 mi [20 km] N Emmett, Gem Co., T8N, R2W, Sec. 12 [44°03′N, 116°32′W, 810 m], 28 February 1982 (ACMNH 224, 236, 237, 238; reported in Baird and Saunders 1992); Dry Creek Road, 1.4 mi [2.2 km] E Little Willow Creek, Payette Co., T4N, R2W, Sec. 18 [44°07′N, 116°37′W, 815 m elev.], 20 February 1983 (ACMNH 318 [10 m, 13 f]), 26 February 1983 (ACMNH 317 [8 m, 3 f]); Weiser Cove, Washington Co. [44°13′N, 116°44′W, 715 m elev.], 7 March 1982

(ACMNH 228, 229, 230); lower Mann Creek, 2.5 mi [4 km] N jct. Weiser River Road, Washington Co. [44°13′N, 116°51′W, 720 m elev.], 14 March 1982 (ACMNH 231, 232, 233, 240, 242, 243, 244); Washington Co., lower Mann Creek, 3.3 mi [5.3 km] N jct. Weiser River Road [44°17′N, 116°51′W, 730 m elev.], 14 March 1982 (ACMNH 239).

This is a very common flea in most of the western United States and western Canadian provinces (Baird and Saunders 1992). Hosts include other western ground squirrels of subgenus *Spermophilus* (Table 1), antelope ground squirrels (*Ammospermophilus leucurus*), woodrats (*Neotoma* sp.), and badgers (Lewis et al. 1988, Baird and Saunders 1992). It was previously recorded from *S. brunneus* by Baird and Saunders (1992).

Thrassis pandorae pandorae Jellison

We found 1 specimen of this flea on *S. b. brunneus* at Lick Creek, Adams Co., T19N, R3W, Sec. 14 [44°54′N, 116°40′W, 1290 m elev.], 17 April 1983 (ACMNH 305 [1 m]).

This flea is distributed from Washington to California and east to Colorado (Stark 1970). It is found most frequently on *Spermophilus armatus*, *S. beldingi*, and *S. elegans* (= *richardsonii* in Stark 1970), but also occurs on *S. columbianus*, *S. elegans* (Table 1), and a variety of other rodents, lagomorphs, and carnivores (Stark 1970). *S. b. brunneus* is a new host record.

Thrassis francisi barnesi Stark

We found this flea on *S. b. endemicus* at Sucker Cr. 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 31 May 1981 (ACMNH 220 [3 m, 4 f]), 3 May 1987 (ACMNH 540 [4 m, 3f], ACMNH 541 [2 m, 1 f], ACMNH 542 [1 m, 6 f], ACMNH 543 [4 m, 7 f], ACMNH 544 [1 m, 1 f], ACMNH 545 [2 m, 1 f], ACMNH 547 [4 m, 9 f], ACMNH 548 [1 f], ACMNH 549 [3 m, 7 f]); 7 mi [11 km] N Emmett, Gem Co., T7N, R1W, Sec. 5 [43°58′N, 116°29′W, 920 m elev], 23 May 1987 (ACMNH 546 [4 m, 2 f]); Sand Hollow, 5.6 km N, 5.0 km E Payette, Payette Co., T9N, R4W, Sec. 7 [44°08′N, 116°51′W, 750 m elev.], 30 March 1989 (USNM 565927 [3 m, 2 f]).

This flea occurs north of the Snake River in western Idaho, and on both sides of the river in eastern Idaho and south into central Utah and eastern Nevada (Stark 1970). Its most common hosts are *S. armatus* and *S. elegans*, rather than *S. townsendii mollis*, the usual host of *T. f. francisi*. Stark (1970) felt that host associations may separate the 2 subspecies of *T. francisi*, although the 2 fleas appeared to intergrade in eastern Nevada. *S. b. endemicus* is a new host record.

Thrassis francisi francisi (Fox)

We collected 14 individuals of this flea from *S. b. endemicus* at 1 locality: Dry Creek Road, 1.4 mi [2.2 km] E Little Willow Creek, Payette Co., T4N, R2W, Sec. 18 [44°07′N, 116°37′W, 815 m elev.], 26 February 1983 (ACMNH 318 [1 m, 5 f], SM2 [2 m, 3 f]), 24 February 1986 (ACMNH 920 [2 m, 1 f]).

This flea is known from the Great Basin desert of eastern Oregon, Idaho south of the Snake River, eastern Nevada, Utah, and parts of Wyoming. It occurs primarily on *S. townsendii*, but the white-tailed prairie dog (*Cynomys leucurus*) is the usual host in Wyoming (Stark 1970). There are incidental records from several species of ground squirrels (Table 1), marmots, and deer mice (Stark 1970). Our records are the 1st from any host north of the Snake River in Idaho (Stark 1970, Lewis et al. 1988, Baird and Saunders 1992); *S. b. endemicus* is a new host record.

Thrassis francisi rockwoodi Hubbard

Two males of this flea were collected from *S. b. endemicus* at a single locality: Sucker Creek, 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 223), 28 February 1982 (ACMNH 227 [2 m]; reported in Baird and Saunders 1992).

This subspecies has been recorded from eastern Oregon, northwestern Nevada, and northern California, where it occurs most commonly on *S. beldingi*, although collections have been made from *S. townsendii* (Stark 1970, Lewis et al. 1988).

Acarina: Ixodidae

Ixodes sculptus Neumann

We collected specimens of this tick from *S. b. brunneus* at 1 locality: OX Ranch 1–2 km S, 1–2 km E Bear, Adams Co. [45°00′N, 116°39′W, 1340 m elev.] (live-trapping collections).

This widespread tick occurs from western Canada south to California and Texas and east across the Great Plains. It occurs on several

western ground squirrels of the subgenus *Spermophilus* (Table 1), prairie dogs (*Cynomys* sp.), marmots, voles (*Microtus* sp.), pikas (*Ochotona* sp.), gophers (*Thomomys* sp.), jumping mice (*Zapus* sp.), domestic animals, and various carnivores (Doss et al. 1974). *S. b. brunneus* is a new host record.

Acarina: Laelapidae

Androlaelaps fahrenholzi (Berlese)

We collected 8 specimens of this mite from *S. b. endemicus* at the following localities: Sucker Cr. 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 227 [4 f, 2 deutonymphs]); lower Mann Creek, 2.5 mi [4 km] N jct. Weiser River Road, Washington Co. [44°16′N, 116°51°W, 720 m elev.], 14 March 1982 (ACMNH 233 [2 f]).

This mite is widespread in Eurasia, North America (Whitaker 1979), and Central America (Strandtmann 1949). It occurs on a wide variety of mammals, including marsupials (*Didelphis* sp.), insectivores, bats, several families of rodents, lagomorphs, carnivores, and birds (Strandtmann 1949, Whitaker and Wilson 1974, Rayburn et al. 1975). Opossums, insectivores, and rodents are the primary hosts, but *A. fahrenholzi* has the least host specificity and widest geographic range of any North American ectoparasitic mite (Whitaker 1979). These are the 1st records from *S. brunneus*.

Nematoda: Rhabditidae

Rhabditis (*Pelodera*) *orbitalis* Sudhaus and Schulte

We observed this parasitic eyeworm only in live-trapped *S. b. brunneus* from OX Ranch 1–2 km S, 1–2 km E Bear, Adams Co. [45°00′N, 116°39′W, 1340 m elev.].

All specimens were collected in April and May 1990 to 1994. We found them in 1 eye or both eyes of yearling and adult *S. b. brunneus*. The number per eye varied from 0 to 1272. The museum specimens were not checked for eyeworms. In 1994, T. A. Gavin and P. W. Sherman examined 21 live-trapped *S. b. endemicus* from Sand Hollow, Payette Co., and found no eyeworms.

This eyeworm has been reported previously from Eurasian and North American voles and lemmings (*Microtus* spp., *Lemmus trimucronatus*, *Dicrostonyx groenlandicus*, *Pitimys subterraneus*, *Arvicola terrestris*, and *Clethrionomys* spp.), mice (*Apodemus* spp. and *Mus musculus*), and rats (*Rattus norvegicus*; Poinar 1965, Kinsella 1967, Cliff et al. 1978, Hominick and Aston 1981, Schulte 1989). *S. b. brunneus* is a new host record, the 1st record of any *Rhabditis* from Sciuridae, and also the 1st record of *R. orbitalis* from Idaho.

Epizootics

In 11 field seasons (April–June) of work with *S. b. brunneus*, we found only 2 dead individuals, and none were observed sick or dying. While a number of populations have declined (T. A. Gavin, P. W. Sherman, and E. Yensen personal observation), mortality occurred while the animals were in hibernation rather than during the active season. The most serious population declines were estimated to be around 50% in 1 yr, rather than the 95%–100% active season mortality typically associated with plague (Lechleitner et al. 1968, Rayor 1985). Although numbers of fleas on individual squirrels were relatively low, especially in *S. b. brunneus*, all flea species we collected are important in plague epidemiology in other hosts (Pratt and Stark 1973) and could potentially play a role in an Idaho epizootic.

Discussion

Collections of ectoparasites from *S. brunneus* have resulted in new state records for the flea *Thrassis francisi rockwoodi* and the eyeworm *Rhabditis orbitalis*, plus 9 new host records. Because there have been no previous studies of *S. brunneus*, the new records are hardly surprising. However, the records of *Thrassis f. francisi* and *T. f. rockwoodi* on *S. b. endemicus* were unexpected. *Thrassis f. barnesi* occurs north of the Snake River in the Snake River Plain (Stark 1970) and is the subspecies of *Thrassis francisi* that would be expected to occur in the range of *S. b. endemicus*. Instead, we found *Thrassis f. francisi*, which is common in *S. townsendii mollis* south of the Snake River, and *T. f. rockwoodi*, for which the nearest locality is from Oregon across the Snake River (Stark 1970), a major biogeographic barrier in southern Idaho (Davis 1939). This interesting situation merits further study.

With the exception of eyeworms, ectoparasites of *S. brunneus* are all known from multiple other species of ground squirrels (Table 1). Thus it is curious that *S. b. brunneus* and *S. b.*

endemicus shared only a single ectoparasite, *Oropsylla t. tuberculata*, a widespread flea found on at least 4 other species of ground squirrels. By contrast, the geographically and taxonomically close (Nadler et al. 1984) *S. townsendii* has all but one of the ectoparasite species found on both *S. brunneus* subspecies. However, *Spermophilus townsendii* is now recognized (Hoffmann et al. 1993) as a complex of 3 closely related sibling species with different karyotypes, and it was not always clear to us from the literature (Table 1) which parasites were associated with which host. Consequently, we have treated *S. townsendii* as a single entity herein.

There are several possible explanations for the lack of shared ectoparasites between *S. b. brunneus* and *S. b. endemicus*: (1) they are geographically separated, and their ranges are inhabited by different ectoparasites; (2) they occur in different habitats and therefore have different ectoparasites; (3) pelage differences between them may be different "microhabitats" for ectoparasites; (4) possibly the formerly shared ectoparasites on one or the other subspecies have been lost via a founder event, due to population structure, or because of population bottlenecks; and (5) we did not adequately sample all ectoparasites on either subspecies. Among these hypotheses, (5) is the least interesting evolutionarily, and (4) is the most interesting.

Most western ground squirrel species are allopatric or parapatric; thus, there is little possibility of direct transmission of ectoparasites among them. Historically, the 2 subspecies of *S. brunneus* were separated by 19 km, 250 m in elevation, and a habitat change from arid shrub-steppe vegetation to montane meadows (Yensen 1991). At present, the nearest extant populations are separated by 48 km. Because *S. townsendii* is allopatric to *S. brunneus*, occurs in nonmontane habitats, and has all ectoparasites found on both subspecies of *S. brunneus*, differences in geography (hypothesis 1) and habitats (2) are unlikely to be the sole explanations for the differences in ectoparasites between *S. b. brunneus* and *S. b. endemicus*.

There are significant differences in pelage length between *S. b. brunneus* and *S. b. endemicus* (Yensen 1991). Interestingly, the pelage of *S. townsendii* is intermediate in length between the 2 *S. brunneus* subspecies (E. Yensen unpublished data). There also appear to be differences in hair density and diameter, although these were not quantified by Yensen (1991). Possibly *S. townsendii* is inhabitable by the entire set of ectoparasites, and each subspecies of *S. brunneus* is a suitable host for about half the set. Thus, pelage differences (hypothesis 3) are a possible explanation for the lack of overlap in ectoparasite species between 2 very close relatives, but it would not explain the differences in parasite loads or the low percentages of nonparasitized individuals.

Anderson and May (1979) argued that parasite infestations should be sensitive to host population structure (hypothesis 4). As population size declines and populations become more isolated, the probability of parasite species loss should increase. Our data were consistent with this pattern: the proportion of parasitized *S. b. brunneus* was significantly lower than that of *S. b. endemicus*; the former has smaller, more isolated populations.

The isolated *S. b. brunneus* populations would also retard exchange of ectoparasites among populations. Thus, there might be stochastic losses of parasite populations with low probability of recolonization (Anderson and May 1979). The differences in incidence of parasites between *S. b. brunneus* and *S. b. endemicus* are consistent with this interpretation.

The low density and wide dispersion of individuals within *S. b. brunneus* populations at a site (E. Yensen and P. W. Sherman personal observation) may also retard direct transfer of ectoparasites, and, consequently, *S. b. brunneus* populations may not be able to support large ectoparasite populations. The low incidence of parasitism in Idaho ground squirrels thus appears to be related to population structure.

Because we did not examine ground squirrels under a microscope, we do not suppose that all ectoparasites were collected (hypothesis 5). However, there was no systematic bias in the sampling that would account for the differences in the proportion of parasitized animals and parasite load differences between *S. b. brunneus* and *S. b. endemicus*. The low proportion of parasitized *S. b. brunneus* (28%) and *S. b. endemicus* (70%) in this study may have been partially because our collecting techniques missed smaller ectoparasites. However, the same techniques were used for both subspecies; therefore, the sampling differences between them should reflect real differences in parasite load. Thus, with the number of animals and

localities sampled, the low overlap in lists of parasites is striking.

Further, the low proportion of *S. brunneus* with ectoparasites (55%), especially in *S. b. brunneus*, is atypical of *Spermophilus*. For example, Hilton and Mahrt (1971) found that in Alberta 100% of *S. columbianus* and *S. franklinii* and 92% of *S. richardsonii* had ectoparasites. We were collecting *S. townsendii* and *S. columbianus* at the same time as *S. brunneus* and were impressed by the much higher parasite loads on those species.

Although we did not observe plague in *S. brunneus* during this study, it does occur in southwestern Idaho. Serum samples positive for *Yersina pestis*, the plague bacterium, were reported from *S. townsendii* during a major ground squirrel die-off in 1941–42 in Ada, Canyon, and Payette counties, immediately south of the range of *S. b. brunneus* (Hubbard 1947, Link 1955). In 1975–1977, positive antibody titers to plague were found in 72%–91% of badgers in the Snake River Birds of Prey Area, 50 km south of the range of *S. b. endemicus* (Messick et al. 1983). Badgers are important predators of ground squirrels. Eight of 9 dead Townsend's ground squirrels examined by Messick et al. (1983) were positive for *Y. pestis*. The plague bacterium has been detected in other species of *Spermophilus* in all 5 Idaho counties where *S. brunneus* populations exist, but until 1995 no *S. brunneus* had been examined (Idaho Department of Health and Welfare personal observation). In April 1995, T. A. Gavin found a dead *S. b. brunneus* at the OX Ranch and sent it to the Wyoming State Veterinary Laboratory (Laramie) where it was assigned case #95W3914. The carcass was found to be negative for *Y. pestis* (E. Williams personal comment). Nonetheless, in the event of a plague epizootic, local populations of *S. brunneus* could easily be decimated. With only a small number of populations remaining, plague could jeopardize the survival of both subspecies of *S. brunneus*.

NOTE ADDED IN PRESS

Six hibernacula of *S. b. brunneus* were excavated in spring 1995 (Yensen and Sherman unpublished data). Nests recovered from the hibernacula were placed in plastic bags in the field, taken to the laboratory, and then placed in Berlese funnels; small invertebrates were collected in 70% ethanol. Only the fleas have been identified to date, but we can now add the following records:

Neopsylla inopina

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [6 m, 7 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [8 m, 7 f]; Adams Co., mouth of Cold Springs Creek, 14 May 1995 [1 m, 1 f].

Oropsylla idahoensis

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [1 m, 2 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [4 m, 2 f]; Adams Co., 3 km S Bear, 16 April 1995 [1 f].

Oropsylla tuberculata tuberculata

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [18 m, 16 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [20 m, 21 f]; Adams Co., mouth of Cold Springs Creek, 14 May 1995 [3 f].

Thrassis pandorae pandorae

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [28 m, 31 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [8 m, 15 f]; Adams Co., 3 km S Bear, 16 April 1995 [1 m].

Catallagia sp., prob. *decipiens*

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [1 f].

Foxella ignota

Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [4 m, 3 f].

Spermophilus b. brunneus is a new host record for *Catallagia* sp. and *Foxella ignota*. *Catallagia decipiens* is widely distributed in the western United States and is usually found on deer mice (Baird and Saunders 1992). *Foxella ignota* is commonly found on pocket gophers in the northern Rocky Mountains (Hubbard 1947).

These new records also indicate that different sets of ectoparasites occur on *S. b. brunneus* and *S. b. endemicus*, thus corroborating the earlier results. The same 4 flea species were again found associated with *S. b. brunneus*, and neither *Catallagia* nor *Foxella* is known from *S. b. endemicus*.

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